Urban ecosystem services at the plant-soil interface

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CONTENTS

ABSTRACT

Continuing urbanization is a crucial driver of land transformation, having widespread impacts on virtually all ecosystems. Terrestrial ecosystems, including disturbed ones, are dependent on soils, which provide a multitude of ecosystem services. As soils are always directly and/or indirectly impacted through land transformation, land cover change causes soil change. Knowledge of ecosystem properties and functions in soils is increasing in importance as humans continue to concentrate into already densely-populated areas. Urban soils often have hampered functioning due to various disturbances resulting from human activity. Innovative solutions are needed to bring the lacking ecosystem services and quality of life to these urban environments. For instance, the ecosystem services of the urban green "infrastructure" may be substantially improved through knowledge of their functional properties.

In the research forming this thesis, the impacts of four plant species (*Picea abies*, *Calluna vulgaris*, *Lotus corniculatus* and *Holcus lanatus*) on belowground biota and regulatory ecosystem services were investigated in two different urban soil types. The retention of inorganic nitrogen and phosphorus in the plant-soil system, decomposition of plant litter, primary production, and the degradation of polycyclic aromatic hydrocarbons (PAHs) were examined in the field and under laboratory conditions. The main objective of the research was to determine whether the different plant species (representing traits with varying litter decomposability) will give rise to dissimilar urban belowground communities with differing ecological functions.

Microbial activity as well as the abundance of nematodes and enchytraeid worm biomass was highest below the legume *L. corniculatus*. *L. corniculatus* and the grass *H. lanatus*, producing labile or intermediate quality litter, enhanced the proportion of bacteria in the soil rhizosphere, while the recalcitrant litter-producing shrub *C. vulgaris* and the conifer *P. abies* stimulated the growth of fungi. The loss of nitrogen from the plant-soil system was small for *H. lanatus* and the combination of *C. vulgaris* + *P. abies*, irrespective of their energy channel composition. These presumably nitrogen-conservative plant species effectively diminished the leaching losses from the plant-soil systems with all the plant traits present. The laboratory experiment revealed a difference in N allocation between the plant traits: *C. vulgaris* and *P. abies* sequestered significantly more N in aboveground shoots in comparison to *L. corniculatus* and *H. Lanatus*. Plant rhizosphere effects were less clear for phosphorus retention, litter decomposition and the degradation of PAH compounds. This may be due to the relatively short experimental durations, as the maturation of the plant-soil system is likely to take a considerably longer time.

The empirical studies of this thesis demonstrated that the soil communities rapidly reflect changes in plant coverage, and this has consequences for the functionality of soils. The energy channel composition of soils can be manipulated through plants, which was also supported by the results of the separate meta-analysis conducted in this thesis. However, further research is needed to understand the linkages between the biological community properties and ecosystem services in strongly human-modified systems.

LIST OF ORIGINAL PAPERS

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I. Vauramo, S. & Setälä, H. 2010: Urban belowground food-web responses to plant community manipulation - impacts on nutrient dynamics. Landscape & Urban Planning 97: 1-10

II. Vauramo, S. & Setälä, H. 2011: Decomposition of labile and recalcitrant litter types under different plant communities in urban soils. Urban Ecosystems 14: 59-70. [DOI: 10.1007/s11252-010-0140-9]

III. Vauramo, S., Jääskeläinen, V. & Setälä, H. 2011: Environmental fate of polycyclic aromatic hydrocarbons under different plant traits in urban soil as affected by nitrogen deposition. Applied Soil Ecology 47:167-175.

IV. Vauramo, S., Kozlov, M., & Setälä, H. 2011: Effects of restorative land-use changes on soil fungi to bacteria ratio. – A meta-analysis approach. Manuscript.

THE AUTHOR'S CONTRIBUTION

I. Corresponding author. SV planned the field trial together with HS. SV performed the laboratory and data analysis and wrote the paper under the supervision of HS.

II. Corresponding author. SV planned and established the field study, performed the laboratory and data analysis, and wrote the paper under the supervision of HS.

III. Corresponding author. SV, HS and VJ planned the laboratory experiment. SV performed the soil faunal analysis and nutrient measurements. VJ analyzed soil and lysimeter water PAHs and performed PLFA analysis with a contribution from SV. SV wrote the paper under the supervision of HS.

IV. Corresponding author. SV planned and wrote the literature review under the supervision of HS. SV performed the statistical analysis with a contribution from MK.

ABBREVIATIONS AND CONCEPTS USED IN THE THESIS AND THEIR DEFINITIONS:

AM	arbuscular mycorrhiza
C	carbon
C/N ratio	carbon-to-nitrogen ratio
ECM	ectomycorrhiza
FAME	fatty acid methyl ester
F/B ratio	fungi-to-bacterial (biomass) ratio
FDR	false discovery rate, a statistical method that corrects for the α inflation/Type I error
GC-FID	gas chromatograph accompanied by a flame ionization detector
GC-MS	gas chromatograph accompanied by a mass spectrometer
MANOVA	multivariate analysis of variance
N	nitrogen
NPP	net primary productivity
OM	organic matter
PAH	polycyclic aromatic hydrocarbon
PLFA	phospholipid fatty acid
SOM	soil organic matter
TOC	total organic carbon

1. INTRODUCTION

1.1 Ecological consequences of urbanization

The continuously growing human population is increasingly concentrating in urban areas. The world urban population exceeded that of rural areas in 2007 (UN, 2008). By 2030, five billion (58.8%) out of the global population of 8.5 billion people will be urban dwellers. Although the land use types characterised as 'urban areas' cover only 1–4% of the global land surface (Schneider et al. 2010), urbanization is by far the largest force impacting land use worldwide (Grimm et al. 2008). However, the term 'urban' is often used by ecologists without further consideration of the definition (Mcintyre et al. 2000), and because of this, it does not fully reflect the complexity of human-dominated urbanized systems (Grove and Burch, 1997). The definition of urban in this thesis is based on the conceptual idea of Hendrix et al. (1988), which refers to physical structures of the city: built-up, high population density environments with a low coverage of unsealed soil surfaces and highly artificial biological communities. It leads to functional impairment of the area. Urban area has been described as human equivalent of the livestock feedlot: A large population of humans living at a high density are supported by biophysical processes mostly occurring elsewhere (Rees, 2003).

Rapid urbanization is considered one of the major forces threatening biodiversity and ecosystem services provided by biological communities (Pickett et al. 2001, Beier et al. 2008). Land-use changes may significantly impact the functionality of ecosystems (Vitousek et al. 1997, Alessa and Chapin, 2008). For example, changes in land use result in fragmentation of natural habitats, an increased spatial load of nutrients and chemicals and an increase in stormwater runoff from impermeable surfaces (Pickett et al. 2001, Pickett and Cadenasso, 2009).

The sprawl of urban settlements will increase pressure on the neighbouring ecosystems of cities (Han, 2010). The urban environment has recently become one of the fastest growing research topics in ecology due to increasing awareness of the importance of ecosystem services for the sustainable development of cities. There are signs of an increased priority on maintaining natural, connected landscapes under the growing pressures of habitat fragmentation (Moilanen et al. 2005). This reflects land use policy, as illustrated by examples from the world megacities. For instance, the forest coverage of the megacity of Istanbul is currently increasing (Karaburun et al. 2010). Revegetation of urban spaces can potentially strengthen the biogeochemical functions of the soil (Lorenz and Lal, 2009). However, the understanding of urban ecosystem services (Tianhong et al. 2010) or the ecological properties of urban ecosystems (Pickett and Grove, 2009) is far from complete.

1.2 Soils as a basis for terrestrial ecosystem services

Ecosystem services are the benefits people obtain from ecosystems (MA, 2003). The interface of aboveground and belowground communities, i.e. the rhizosphere of plants, is important for a number of regulating, supporting and provisioning ecosystem services (Barrios, 2007). Biogeochemical and hydrological cycles, soil structure formation, carbon storage, the decomposition of detritus, mineralization and retention of nutrients and detoxification of contaminants are largely regulated or affected by soil communities (Hooper and Vitousek, 1997, Wolters et al. 2000). It has been estimated that soils store about 70% of global terrestrial carbon, more than twice

the amount stored in living biomass (IPCC, 2007). However, the size of the deeply stored soil inorganic and organic carbon stocks may be still underestimated in the current global carbon budget (Díaz-Hernández, 2010).

Since 1850, anthropogenic land-use changes have resulted in a massive loss of soil organic carbon (124 Pg), contributing approximately one-third of the total increase in atmospheric CO_2 (Foote and Grogan 2010). As the world economy increasingly searches for carbon-efficient solutions to maintain the growing human population, the importance of the soil carbon stock in the global carbon budget should be highlighted (Singh et al. 2010).

Biological communities of above- and belowground subsystems are closely interlinked, which reflects the functions of the terrestrial ecosystems (Brussaard, 1998, Barrios 2007). The broad spectra of above-belowground species interactions include both mutualistic and antagonistic relationships (Wardle et al. 2004). Although soils are generally considered to be resilient in their basic functions (Setälä et al. 2000, Fitter et al. 2005), single keystone species, such as enchytraied worms in boreal forests, may be extremely important for ecosystem services in resource-depleted or environmentally harsh conditions (Salminen et al. 2002). Symbiotic relationships between plants, mycorrhizal fungi (AM, ECM, ericoid mycorrhiza) and N-fixing rhizosphere bacteria are a fundamental part of plant nutrient uptake (Barea et al. 2002). Furthermore, plant biodiversity is likely to foster the biomass of soil microbial decomposers, especially in soils with a low initial nutrient content (Zak et al. 2003).

Successional shifts of plant communities affect the belowground food-web structure (Pennanen et al., 2001, Zeller et al. 2001). However, belowground succession may take substantially longer than shifts in vegetation structure (van der Wal et al. 2006). Historical land use has been found to create a legacy that controls the belowground community composition and function (Schaefer 2009, Davies and Hall 2010).

Evidence has accumulated of the existence of functionally different energy channels below recalcitrant versus labile litter-producing plants (Wardle et al. 2004, Bardgett et al. 2005). The energy from primary production flows through three distinct food-web compartments: bacterial, fungal and root energy channels, which are coupled by higher trophic groups (Moore and Hunt, 1988; Fig. 2). These distinct soil energy channels are presumed to affect the nutrient and carbon dynamics of the plant-soil systems, as the energy should flow more slowly through the fungal energy channel than the faster bacterial-based channel (Moore et al. 2005).

The magnitude and even the direction (symbiotic vs. antagonistic) of plant-soil interactions may change due to shifts in environmental abiotic characteristics, such as nutrient status (Haase et al. 2008). Due to the complex nature of biotic and abiotic interactions, it is evident that a better understanding of the above-belowground linkages is needed to make reliable predictions of the impacts of global climate change on key soil ecosystem processes (Tylianakis et al. 2008, Bardgett and Wardle 2010, Bezemer et al. 2010).

1.3. Impacts of land-use changes on the functionality of soils

Global climate change is fundamentally affecting land use (Lamptey, 2010). Since the modification of land-use activities ultimately involves the exploitation of soils, land-use changes can be seen as analogous to soil-use changes (Pouyat et al. 2007). An alteration in land use will have impacts on the vegetation structure and coverage (Pickett et al. 2001, Botham

et al. 2009), which can cascade to the belowground communities (Pavao-Zuckerman and Byrne, 2009).

Rapid human population growth in concert with the increase in fossil-fuel combustion and intensification of agricultural and forestry practices has caused high inputs of N in densely populated areas (Holland et al. 2005). Consequently, anthropogenic activities produce over 50% of global emissions of reactive nitrogen (Vitousek et al. 1997). Since terrestrial ecosystems are commonly nitrogen-limited (LeBauer and Treseder, 2008), an increase in the amount of easily available nitrogen forms evidently exerts various cumulative impacts on ecosystems (Wang et al. 2010). Chronic nitrogen deposition increases the risk of soil nitrogen saturation and leaching losses, especially from soils with a low (< 25) C/N ratio (Macdonald et al. 2002). Soil sealing, i.e. the creation of impermeable surfaces, greatly reduces the natural hydrological and biogeochemical cycles in densely built urban areas (Lorenz and Lal, 2009). The nitrogen retention capacity of urban soils can also vary according to physico-chemical properties of the urban land cover (Pouyat et al. 2007), as well as among cities with different land use histories (Pouyat et al. 2008).

Nitrogen enrichment of soils has profound impacts on soil communities, as the energetic basis of many mutualistic relationships between plants (hosts) and their belowground counterparts (symbionts) is in the nitrogen limitation of plants. Nitrogen fertilization has been found to change the community structure of arbuscular mycorrhizal symbionts (Egerton-Warburton et al. 2007), and reduce the abundance of mycorrhizal symbionts (Treseder, 2004). However, there is a discrepancy in the effects of nitrogen treatment on the mycorrhizal biomass (Treseder et al. 2007, Garcia et al. 2008). The adverse effects of N fertilization on soil fungal communities are not always evident. For instance, Bardgett et al. (1999) observed a microbial community shift in favour of fungi after N amendment (equalling 100 kg ha^{-1} N fertilization rate) in N-deficient grassland soil.

Although the impacts of divergent land-use types on soil microbial properties have been described (Fierer et al. 2009), little is known about the soil community properties under rapidly changing land use (Moore et al. 2005). The soil fungal-to-bacterial ratio has been used as an indicator of the developmental stage of the soil (Bardgett et al. 2010). A high F/B ratio is considered to indicate the maturity of the ecosystem, whereas a low F/B reflects an early stage of ecosystem succession (Wardle et al. 2004). However, the shift in dominance from the bacterial energy channel towards the fungal energy channel has not been comprehensively studied under changes in land use.

2. OBJECTIVES OF THE PRESENT STUDY

The aim of this research project was to examine how the linkages between aboveground and belowground biota affect the ecosystem services of urban soils. Manipulative experiments using plants with different litter quality traits were conducted in two urban soil types. Litter decomposability was hypothesized to affect the soil food-web structure, creating either bacterial-based or fungal-based belowground energy channels. Plants producing recalcitrant litter were hypothesized to create a fungal-based energy channel with a high nitrogen retention capacity. Plants with labile/intermediate quality litter were hypothesized to promote the establishment of a leaky, nitrogen-leaching bacterial-based energy channel.

The plant traits were hypothesized to create belowground communities that would decompose their own litter type

most efficiently (II). This 'home-field advantage' hypothesis (Ayres et al. 2006) was tested in both urban soil types.

The effects of the plant traits on the environmental fate of polycyclic aromatic hydrocarbons (PAHs) and labelled nitrogen (^{15}N) were investigated in the laboratory. Vegetation has been shown to affect the degradation of organic pollutants such as PAHs (Lee et al. 2008). The high rhizospheric activity of legumes was hypothesized to affect the degradation of added contaminants. Furthermore, the PAH leaching losses and soil extractable content of PAHs was predicted to be affected by nitrogen addition. The extra nitrogen was hypothesized to increase the degradation of PAH compounds in soils, therefore reducing their leaching.

The impacts of vegetation change on soil energy channels were examined by conducting a meta-analytical literature review. The aim of the meta-analysis was to reveal whether the soil fungal-to-bacterial (F/B) ratio, a commonly used soil community parameter, reliably reflects the developmental stage of the ecosystem during land use change.

The main research questions of the thesis were: Do different plant traits create dissimilar rhizosphere communities in urban soils (I, II, III)? Are the different urban plant-soil communities functionally equivalent (I, II, III)? Is the fungal-to-bacterial biomass ratio affected by restorative land use changes (IV)?

The main hypotheses were accordingly:

1) Plant traits producing recalcitrant litter create fungal-based belowground communities, while plants producing labile or intermediate litter support bacterial-based energy/nutrient channels (I).
2) Fungal-based belowground communities are more efficient in retaining nutrients and/or contaminants in comparison to bacterial-based energy channels (I, III).
3) Plants create a belowground subsystem that is best suited for the breakdown of their own litter type (II).
4) The fungal to bacterial biomass ratio increases after successional, restorative land use change (IV).

3. MATERIAL AND METHODS

3.1 Field experiments

The impacts of different plant types on urban soil biology and biogeochemical functions were investigated at two field sites with distinct soil quality (referred to as land-fill and garden soil, see Fig. 1; I, II). The sites were situated approximately 2 km from the city centre of Lahti, Southern Finland. Lahti is the eighth largest city in Finland with over 101 000 inhabitants (747 ind.$^{-1}$ km^2) (Lahti, 2010). The chemical and physical properties, age, management history and plant communities of these sites were very different. The landfill site represented typical young 'artificial urban land' consisting of coarse sand and calciferous construction materials and was filled in during 2001–2002. This soil had a low organic matter (2%) and nitrogen content and high pH (7.6 $\pm$ 0.2). Landfill soils are typical to newly constructed urban areas.

The garden soil site was located in Lahti City Gardens, where the soil was classified as fine silt with a much higher percentage of organic matter (9% OM) and a somewhat higher nutrient level in comparison to the landfill soil (I). The garden soil had a pH of 6.3, which is characteristic of horticultural soils. This site had been used for gardening and as a tree nursery for the previous 40 years, and for agricultural purposes before that.

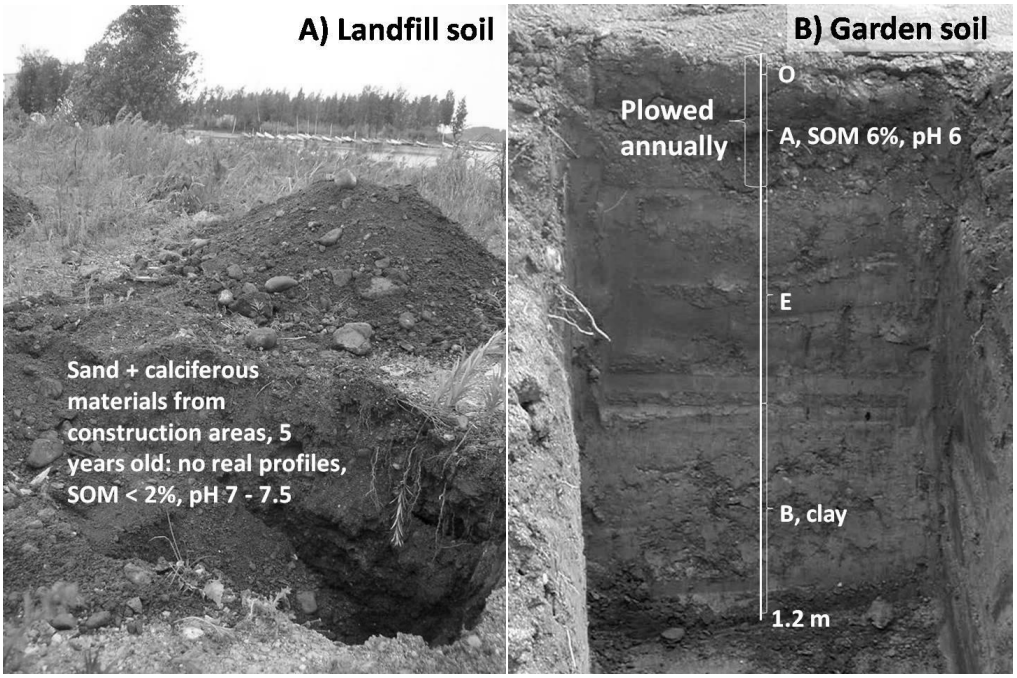

Figure 1. Properties of the two field sites: A) landfill soil and B) garden soil.

Thus the garden soil may be referred to e.g. soils of urban botanical gardens or parks. The horizontal structure of the soils at both sites was disturbed (Fig. 1). Both of the sites were subjected to experimental manipulations in June 2004 by constructing various plant communities in plots on the soil. Plant species producing recalcitrant litter, the conifer *Picea abies* [L] Karst. (Pinaceae) and the shrub *Calluna vulgaris* [L] Hull. (Ericaceae), were planted in the same plot to create a boreal plant mixture, while the legume *Lotus corniculatus* L. (Fabaceae), with labile litter, and the grass *Holcus lanatus* L. (Poaceae), with intermediate litter decomposability, were planted in their own plots. Mixed plant community plots consisted of all three plant types. Weeded, bare soil plots were left as plant-free controls. All five plant treatment plots were replicated five times at both study field sites, producing 25 plots per site. A lysimeter system was installed underneath each plot to collect the water percolating through the soils (I).

The study sites were sampled three times (June, August and October/ November) in 2005 and 2006. Separate soil samples were taken for the analysis of soil faunal community structure (nematodes, enchytraeid worms, microarthropods), PLFA and nutrient concentrations. Lysimeter water samples for the analysis of nitrogen and phosphorus were taken in August 2005, August 2006 and November 2006.

A reciprocal litterbag experiment was established as a part of the field trial in July 2005 (II). Litter from each plant type (I) was placed on every plant treatment plot at both field sites. Separate litterbags were installed for analysis of the litter decomposition rate and soil faunal community composition. The garden soil was sampled 18 weeks (Nov. 2005) and the landfill site 38 weeks (May 2006) after the establishment of the litterbag experiment.

3.2 Laboratory experiment

To explore the impacts of plant type on the fate of nitrogen and organic contaminant deposition, a study was conducted in the laboratory (III).

Mesocosm-scale (0.196 m^2 area, N = 8) containers were divided into five sections that received the same plant treatments as used in the field experiment: *Holcus lanatus, Lotus corniculatus, Picea abies, Calluna vulgaris* and a plant-free control (inner section). However, in this experiment, *P. abies* and *C. vulgaris* were grown in separate areas, and the laboratory experiment lacked the mixed plant community of the field study. Urban soil from the landfill area was used as the growth medium. A lysimeter system was installed underneath each plant community to collect the water percolating through the rhizosphere. The mesocosms were placed in a water bath with temperatures modified according to the growth period (water/air temp.: summer 10/23 °C, autumn or spring 8/15 °C, winter 5/8 °C.). (For further details see Witt and Setälä, 2010). The experiment continued for three full plant growth periods.

At the beginning of the third growth period (during the 'spring'), six (of eight) randomly selected containers received 3.9 mg $^{15}NH_4{}^{15}NO_3$ dissolved in 1 mg ml^{-1} distilled water, equating to a nitrogen deposition rate of 5 kg ha^{-1} typical of Southern Finland. In addition, all mesocosms received phenanthrene and pyrene-spiked soil (10 µg pyrene, 10 µg phenanthrene g^{-1} dry soil) at the beginning of the third growing season. The amount of PAH spiked soil was roughly equivalent to the PAH concentration of street dust in central Copenhagen (Johnsen et al. 2006) and was applied to the intact area of the different plant treatment sectors.

3.3 Meta-analytical literature review

In addition to the experimental studies, a meta-analysis was performed to reveal the impacts of land-use/vegetation change on the soil F/B ratio (IV). Published studies were identified from the Web of Science/ CSA Illumina up to August 2010. The impacts of the following categories of land-use change on the soil F/B ratio were compared: a) from agricultural land to grassland, b) from grassland to heathland, c) from grassland to deciduous forest, d) from grassland to mixed/coniferous forest and e) from deciduous forest to coniferous forest. The purpose of this review was to determine whether 'restorative' land-use changes, i.e. changes aiming towards natural land use types, increase the F/B ratio of soils, as is generally assumed.

3.4 Biological and physico-chemical analyses

3.4.1. Plant NPP and SOM

The aboveground biomass of *L. corniculatus* and *H. lanatus* were estimated from an area of 24 cm x 31 cm in November 2006 by cutting the plant shoots at a height of 5 cm (I). The removed plant material was oven-dried (60 °C) and weighed. The shoot biomass of *C. vulgaris* and *P. abies* were measured from the entire plot area in June 2007. For the analysis of root biomass, three soil cores (area of 10cm^2, depth 15 cm) were taken from each plant treatment plot (I).

The soil organic matter (SOM) content was analyzed from homogenized, oven-dried (+90 °C, 18 h) samples after being incinerated at 550 °C for 4 h (I).

3.4.2 Soil microbial biomass, activity and community structure

The soil microbial community structure and an estimate of its biomass was determined by PLFA analysis as described by Frostegård et al. (1993), with slight modifications presented by Stoeck et al. (2002) (I, III). Briefly, 2 g of freeze-dried soil was used for lipid extraction with Blight and Dyer solution (Blight and Dyer, 1959). Phospholipid fractionation with silica gel columns

(Varian, Bond Elut-SI, 500 µl) was followed by mild alkaline hydrolysis. The resulting FAMEs were analyzed using GC-FID (6890N Network GC System, Agilent Technologies) combined with a 30 m long low-polar capillary column (ZB-5ms, Phenomenex, Torrance, CA, USA). The retention times of different fatty acids were previously verified with GC-MS (Shimadzu, Kyoto, Japan) and a selected ion monitoring (SIM) program.

Soil microbial activity was determined by net carbon mineralization (III) using an Easy Quant Universal Carbon analyzer.

3.4.3 Soil fauna analysis

Soil nematodes and enchytraeid worms (I, III) were extracted using the wet-funnel method (O'Connor, 1967). Soil samples of 10 g and 30 g were taken for nematode and enchytraeid worm analysis, respectively. The extracted nematodes and enchytraeid worms were counted alive within two days. To determine the enchytraeid worm biomass, the formula of Abrahamsen (1973) was applied (I).

The trophic group composition (bacterial- and fungal-feeding nematodes, omnivores, predators and plant parasitic nematodes) was analyzed according to the method described by Yeates et al. (1993) from fixed samples (heated and fixed in 40% ethanol) using a phase contrast microscope at 100-fold magnification.

3.4.4 Soil energy channel biomass

The biomass (C µg g^{-1} OM) of the following food-web compartments was estimated: fungal (fungi and fungal feeding nematodes), bacterial (bacteria and bacterial feeding nematodes) and root (root feeding nematodes) (I). To convert nematode numbers to biomass (ng C per worm) the data of Neher et al. (2004) were applied. The data presented by Klamer and Bååth (2004) were used to convert fungal PLFA 18:2ω6,9 to fungal biomass C, and the data of Bååth and Anderson (2003) to convert the sum of bacterial PLFAs to bacterial biomass C. Omnivorous species (enchytraeids, omnivorous nematodes), predators, and groups with very few observations (microarthropods) were not included in the analysis.

3.4.5 Chemical analyses

Impact of plant type on soil nutrient status and leaching losses was investigated in the field (I) and in a laboratory experiment (II). Potentially leachable soil inorganic nitrogen compounds (NO_3^-, NH_4^+) were extracted with 1M KCl by shaking for 3 h in a planar shaker. PO_4^{3-} was extracted in a similar manner, except that distilled water was used instead of KCl. After extraction, the samples (incl. lysimeter water samples) were filtered through cellulose filter papers (Whatman S&S 597 and 589[3]) to remove soil particles. Soil-extractable nutrients and lysimeter nutrients were analyzed colorimetrically using a QuickChem 8000 analyzer (Lachat Instruments, methods 12-107-04-1-E and 10-115-01-1-B). Total organic carbon (TOC) was analyzed from lysimeter water samples using an Apollo 9000 TOC analyzer (Teledyne Tekmar, standard method SFS-EN-1484).

The plant litter C/N ratio was determined using a Leco CNS-2000 (Leco Corporation, USA) analyser (II). For the analysis of N uptake by the plants, oven-dried plant shoot material was ground in a mill (Retsch MM200, Germany) for 5 minutes at 2000 rpm (III) The ^{15}N analysis (III) was performed at Kompetenzzentrum Stabile Isotope Laboratory (University of Göttingen, Germany) using isotope mass spectrometry (Finnigan MAT, Bremen, Germany).

Potentially bioavailable phenanthrene and pyrene fractions (i.e.

desorbed and non-desorbed forms) in soil were extracted with a mild procedure using organic solvents (Eronen, 2008) (III). Phenanthrene and pyrene compounds were extracted from the lysimeter water samples using ENVI^{TM}-18 DSK 47mm SPE disks (Supelco, Bellefonte, PA). Phenanthrene and pyrene compounds in soil and lysimeter water samples were determined using GC-FID (6890N Network GC System, Agilent Technologies).

3.5 Figures

The biomass (µg C g^{-1} SOM) of the fungal, bacterial and root energy channels (Fig. 2) was applied directly from the estimations given in article I.

The soil inorganic nitrogen content (µg NO_3^+ + NH_4^- g^{-1} dry soil) under the plants with different traits grown in landfill soil (Fig. 3a) was analyzed in article I. To calculate the annual inorganic nitrogen (NO_3^+ + NH_4^-) leaching losses from the different plant treatments grown in landfill soil (Fig. 3b.), data on N leaching losses (I) and the number of frost-free days (215 d) in Southern Finland (Jylhä et al. 2008) were used. The annual N sequestration in the above- and belowground plant biomass (Fig. 3c.) was calculated using the biomass data from article I and C/N data of the plant traits from article II.

Annual carbon sequestration (g C m^2 yr^{-1}) in the shoots and roots by the different plant types was calculated using the biomass data of article I and C/N data of article II (Fig. 4). The soil CO_2 production rate (µg CO_2 h^{-1} g^{-1} dry soil) of the different plant-soil systems was applied from article III (Fig. 5).

3.6 Statistical analysis

Due to heterogeneous variances and the skewed distribution of the datasets (I, II), a non-parametric two-factor Kruskall-Wallis test (Ranta, 1989) was applied to test the main effects of 'plant treatment' and 'soil type' (I) and 'plant treatment' and 'litter type' (II). Since time cannot be properly analyzed with non-parametric tests, the FDR method (Benjamini and Hochberg, 1995) was applied to control the type I error (α inflation) generated by multiple testing (I). This method was not applied for the data of article II because of the substantially lower number of individual tests performed.

The plant treatments were interdependent in the laboratory experiment (III). Therefore the non-parametric Friedman test was chosen for the analysis of plant treatment impacts on the soil fauna abundance, nutrient content and leaching losses of nutrients at the first sampling. At the second sampling, the two-factorial experiment ('plant treatment' and 'N addition' as fixed factors) was analyzed with the two-factor Kruskall-Wallis test (Ranta, 1989). The Friedman test and Wilcoxon Signed Ranks test were used for the analysis of ^{15}N uptake by the plants.

In the meta-analysis (IV), Hedges' *d* statistic (Hedges and Olkin, 1985) was chosen for the calculation of effect size metrics due to its properties that correct for the bias produced by small sample sizes. Random-effects meta-analysis was used, since the studied effect sizes were considered to be sampled from a distribution of effect sizes. To estimate the sensitivity of the meta-analysis results to non-significant test results, Rosenthal's Fail-Safe numbers (Rosenthal, 1979) were calculated for the significant effects.

4. RESULTS AND DISCUSSION

4.1 Effects of urban soil type on plant-soil systems

The urban soil type (artificial landfill soil vs. established urban garden soil) exerted little influence on the composition and functionality of the different plant-soil

systems (I). The plant traits created similar decomposer communities at a roughly equal rate in the different soils (I, II), which contradicts the soil type-specific plant treatment impacts observed by Marschner et al. (2004). The soil structure and fertilization legacy had a small impact on the belowground succession in the current study. Although soil type did not affect the soil microbial biomass as measured by PLFAs (I), the decomposition rate of various litters was higher in garden soil (II). The mechanism behind this observation remains unresolved, but it may be related to the differences in the nutrient status of the two soils. The low N content of landfill soil may retard the degradation of litter in the early phase of decomposition (Berg and Staaf, 1980, Couteaux et al., 1998).

Since intrinsic differences between the biogeochemical characteristics of urban soils are thought to exceed the differences between soils under different land use (Schleuß et al. 1998, Peltola and Åström, 2003, Kaye et al. 2006), it is expected that the urban soil type should have a large impact on the urban ecosystem functions. The ageing of urban soils has been shown to increase the soil microbial biomass and potential C and N mineralization (Scharenbroch et al. 2005). Interestingly, a recent landscape metrics simulation (Jenerette and Potere, 2010) suggested that the variation between different types of urban environments is decreasing. This could mean that the patchiness of urban soils is decreasing and the soil biogeochemical functionality across urban biomes is becoming more homogenous.

4.2 Plant trait effects on the urban soil communities

The selected plant traits (grass, legume, conifer + shrub) had an immediate influence on the belowground communities in urban soils. Although the two soil types (garden and landfill soil) had a distinct land-use history, the plant treatments affected the belowground communities in a similar manner. The leguminous plant (*L. corniculatus*) had the most distinct impact on belowground community composition. This is evidently due to the N-rich litter that is widely known to provide a labile resource for the rapidly multiplying soil bacteria and microbial feeding soil fauna (Griffiths, 1990). Supporting this view, the bacterial biomass and microbial activity was highest in soils growing *L. corniculatus* (I, III). Furthermore, as compared to soils growing *H. lanatus* or *P. abies* and *C. vulgaris, L. corniculatus* increased the abundance of soil nematodes and enchytraeid worms in both urban soils. This is in accordance with previous findings suggesting that nitrogen-fixing plants support larger and more diverse nematode and earthworm communities than grasses, crop plants or shrubs (Griffiths, 1990, Viketoft et al. 2009, Witt and Setälä, 2010).

Besides the overall increase in the abundance/biomass of the heterotrophic soil fauna, the plant traits may affect the belowground community structure (Wardle et al. 2004). The observed higher abundance of bacterial feeding and plant parasitic nematodes under leguminous plants in comparison to other grassland or boreal plant species (I) corresponds to the findings of Viketoft et al. (2009) and Witt and Setälä (2010). Consequently, Milcu et al. (2008) suggested that legumes appear to be keystone species affecting decomposition processes in grasslands.

The selected plant traits had an impact on the composition of soil energy channels (I). The rhizosphere soil of *H. lanatus* and *L. corniculatus* had a significantly higher bacterial channel biomass in comparison to bare soils or *C. vulgaris* and *P. abies* soils (Fig. 2). The root energy channel biomass of mixed communities was significantly higher in comparison to *C. vulgaris* and *P. abies* or bare soil. Although the fungal energy

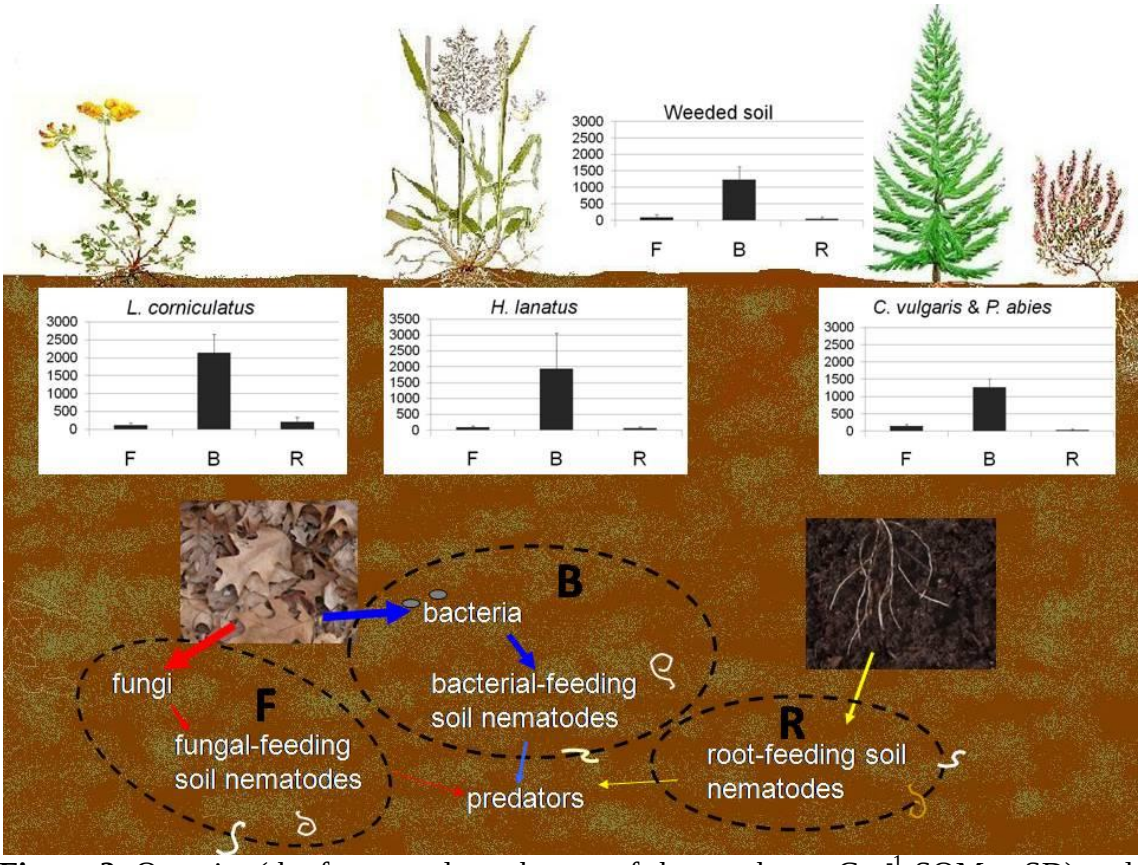

Figure 2. Quantity (the four panels at the top of the graph; µg C g^{-1} SOM + SD) and composition of the three energy channels (F, B, R = fungal, bacterial and root energy channel) in the rhizosphere of *L. corniculatus*, *H. lanatus* and a mixed community of *C. vulgaris* and *P. abies*, and in weeded, bare soil.

channel biomass remained unaffected by the plant treatment, the F/B ratio of C. vulgaris and P. abies rhizosphere soil was significantly higher than that of the other plant treatments (I). Furthermore, the mixed *C. vulgaris* plus *P. abies* litter supported a significantly higher abundance of fungal-feeding collembolans than grass or legume litter (II). Since collembolans have been observed to have feeding preferences for fungi (Berg et al., 2004), this indicates an increasing fungal energy channel biomass. Furthermore, the soil underneath *C. vulgaris* and *P. abies* had a higher F/B ratio in comparison to the rhizosphere of *H. lanatus* or *L. corniculatus* (I). These findings support the first hypothesis that plants producing recalcitrant litter enhance the biomass of the soil fungal energy channel, while those with labile/intermediate quality litter (*H. lanatus*, *L. corniculatus*) favour the build-up of the bacterial channel. As the early aboveground-belowground interactions may have long-lasting impacts on the community composition of soils (Bezemer et al. 2010), the selection of pioneer plants for urban soil restoration should be made consciously.

4.3 Regulating ecosystem services

4.3.1 Retention of bioavailable nitrogen forms by the plant communities

The nitrogen dynamics of the urban soils, determined as the ability of the plant-soil system to retain or leach NH_4 and NO_3, was affected by the plant treatment, while soil phosphorus remained largely

unaffected (I, III). As expected, the legumes increased the soil mineral nitrogen content and leaching losses of ammonium and nitrate from soils (Fig. 3a, b), which supports the second hypothesis. This is in accordance with the results of Scherer-Lorenzen et al. (2003), suggesting that high nitrate leaching losses are characteristic of soils growing leguminous plants in pure cultures.

As soil energy channels differ in their resource use profiles (Moore and de Ruiter, 1991, Debruyn et al. 2007), it is plausible to deduce that the shifts in the food web composition under different plant traits have consequences for the material dynamics of the plant-soil systems. However, all plant-soil systems with a presumably high nitrogen demand (*H. lanatus*, *C. vulgaris* + *P. abies*), irrespective of the bacterial energy channel biomass, created an N conservative system (I). Proportionally, however, the mixed communities containing all plant species retained the highest amount of nitrogen compounds, thereby having the most conservative N economy. This suggests that the N retention capacity of the *H. lanatus*, *C. vulgaris* + *P. abies* rhizosphere was enhanced by the additional N supply provided by the legumes. Interestingly, all plant traits appeared to reduce the leaching of N from newly established systems in comparison to plant-free, bare soils (I), indicating that plant coverage, irrespective of the plant trait, can diminish nutrient losses soon after soil physical disturbance.

The laboratory experiment revealed a difference in the nitrogen sequestration potential between the plant treatments (III). The recalcitrant litter producing *C. vulgaris* and *P. abies* sequestered a significantly higher proportion of added N in their aboveground plant parts in comparison to *L. corniculatus* or *H. lanatus* with intermediate litter quality (Fig. 3c). Findings from both the field and laboratory studies may have some applied value: The differential N sequestration and retention potential of various plant traits should be taken into account when considering the possibilities for the management of nutrient dynamics in disturbed urban soils.

4.3.2 Decomposition of plant litter

The plant treatment, i.e. the community composition of the living plants, had no influence on the decomposition rate of different plant litters (II). Thus, the 'home field advantage' hypothesis 3, suggesting that the rate of plant litter decomposition is influenced by the plant rhizosphere where it resides and is fastest in its own belowground environment (Ayres et al. 2006, Ayres et al. 2009), was thus refuted. In each plant-soil system (including the bare soil), *L. corniculatus* litter decomposed faster than (i) *H. lanatus* litter with intermediate quality, (ii) a litter mix (of all the litter types) or (iii) the recalcitrant *C. vulgaris* + *P. abies* litter. The comparable decomposition rate of litter material in different plant-soil systems suggests relatively similar abiotic and biotic conditions in these soils. This contradicts the prevailing understanding that plant coverage has positive effects on the soil decomposition process (Krift et al. 2002, Subke et al. 2004). The lack of plant treatment impacts on litter decomposition in carbon-poor urban soils was unexpected, as the litter types were found to differentially attract the decomposer fauna (II).

The decomposition rate of the litter mix was intermediate, showing no evidence of non-additive positive or negative (Hector et al. 2000, Ball et al. 2009) effects of litter mixing.

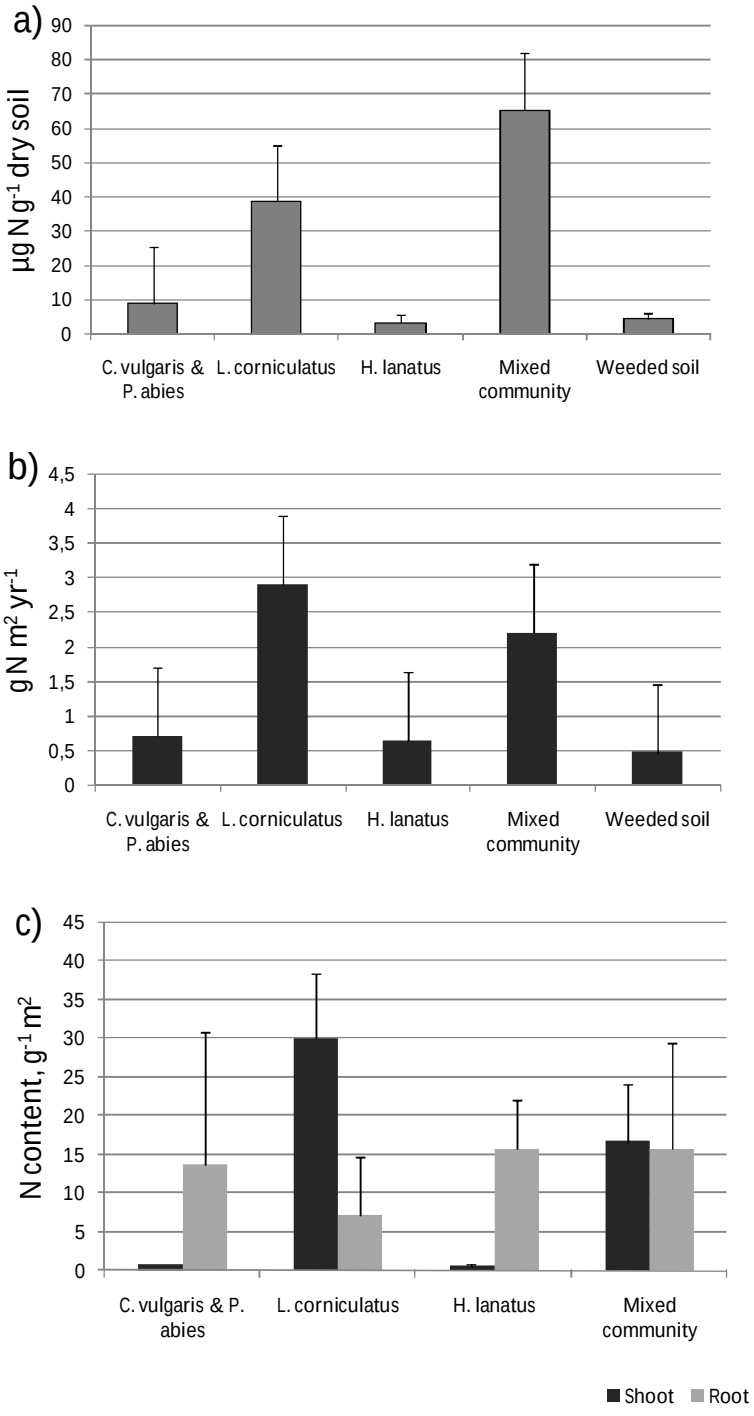

Figure 3. (a) Soil inorganic nitrogen concentration (mean + SD) in the rhizosphere/soil of the plant communities, (b) annual inorganic nitrogen leaching loss (mean + SD), and (c) the annual nitrogen sequestration (mean + SD) in above- and belowground biomass.

4.3.3 Formation of soil organic carbon pool

It is likely that manipulation of the aboveground communities did not influence the size of the soil organic carbon pool due to the relatively short experimental time (3 yrs) (I). However, the differences between plant treatments in carbon sequestration in roots and shoots (Fig. 4) imply that the plant-soil systems differed in their carbon allocation. Rapidly growing legumes allocated higher amounts of carbon to their aboveground plant parts, while grasses, shrubs and conifers seemed to have a larger carbon pool in their extensive root systems belowground.

Since the degradation rate of the plant litter types differed significantly (II), it is presumable that plants with recalcitrant or intermediate litter quality will increase the proportion of undecomposed organic material in their rhizosphere soil, therefore enhancing the soil organic carbon content in the long term. Foote and Grogan (2010) calculated that an abandoned carbon-poor agricultural soil sequestered around 10 g C m^{-2} y^{-1} in the top 10 cm of soil when allowed to naturally revert to mixed hardwood-conifer forest. The estimated soil carbon sequestration potential of young seedlings of all the studied plant traits in this research exceeds these values by several fold (Fig. 4). It is to be noted, however, that the whole carbon balance of the experimental plant-soil systems was not monitored. The slower decomposition rate of recalcitrant litter types may indicate higher carbon accumulation under *C. vulgaris* + *P. abies* in comparison to *L. corniculatus* or *H. lanatus* in the long term. Supporting this view, Strickland et al. (2010) observed slower soil carbon mineralization rates of loblolly pine (*Pinus taeda*) plantations or mature oak (*Quercus sp*.) stands in comparison to agroecosystems. However, due to the intensive management practices needed, the net carbon balance in afforested *Picea marianara* plantations has been found to turn positive only after two decades (Gaboury et al. 2009). Thus, it is not realistic to expect high net carbon sequestration in newly established urban plant-soil systems (but see the estimates of green roof CO_2 absorption by Li et al. 2010); rather, the older urban green spaces may act as C sinks.

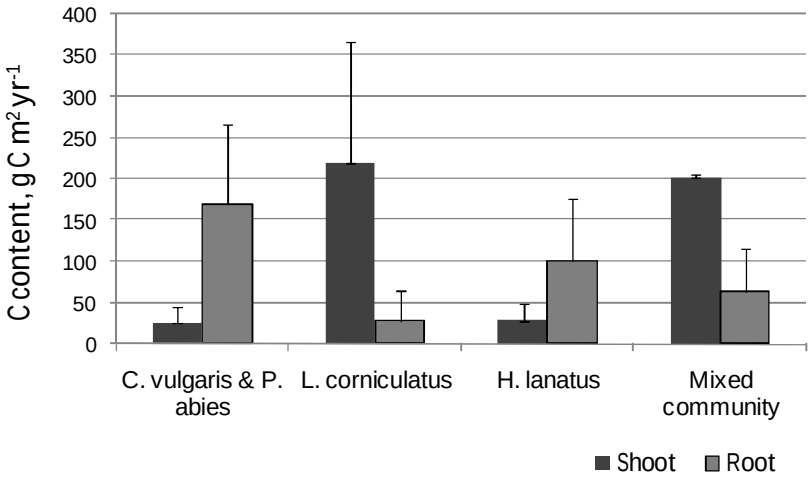

Figure 4. Estimated annual carbon sequestration (mean + SD) in the shoots and roots by the different plant types.

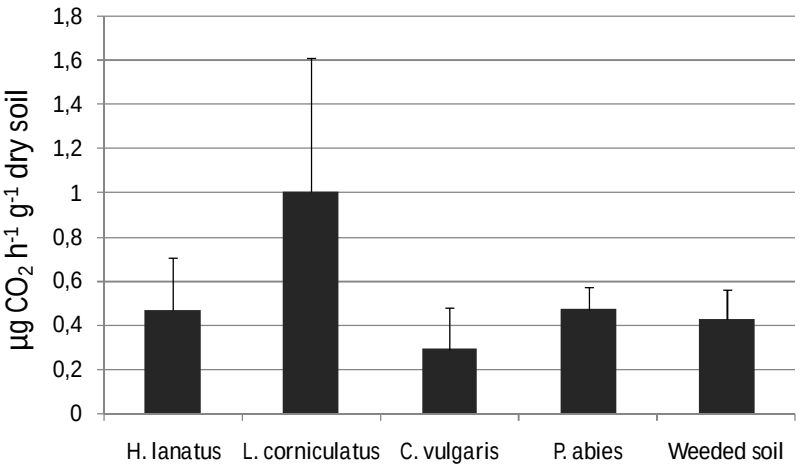

Figure 5. Soil CO_2 production rate (mean + SD) of the different plant-soil systems (III).

4.3.4 Retention and degradation of PAH compounds

In contradiction to hypothesis 2, the higher microbial activity in the rhizosphere of the legume (*L. corniculatus*) (III, Fig. 5) affected neither the quantity of soil-adsorbed PAHs (phenanthrene, pyrene) nor the PAH leaching losses (III). Thus, the short-term laboratory experiment with spiked PAHs did not support previous studies showing that plant types enhancing microbial activity show higher rhizospheric PAH degradation rates (Chaudhry et al. 2005). The lack of impacts of plant treatment on PAH dissipation from urban soils may have been due to the shortage of replicates, the experimental methodology or the relatively short duration of the experiment. However, plants have been shown to reflect the mineralization of PAHs in the early stages of contamination (Lee et al., 2008). Interestingly, there was a lower leaching loss of phenanthrene from soil with added nitrogen, indicating that a relatively minor N addition may affect the mobility of PAHs in urban soils, irrespective of the plant coverage. However, more research is needed to confirm this.

4.4 Soil fungal-to-bacterial ratio as an indicator of soil maturation

In the meta-analysis, the soil fungal-to bacterial ratio was found responsive to the effects of the studied restorative, i.e. successional, land use changes (IV). The impact of land use change on soil was most notable when grasslands were converted to coniferous forest, resulting in an increased F/B ratio. This is in accordance with the prevailing understanding of the energy channel composition of grassland and coniferous forest soils (Moore et al. 2005). The use of the soil F/B ratio as an indicator of the successional stage of soils can thus also be justified on the grounds of the analysed land-use change data. Importantly, the results of the urban field experiment (I) support also this view.

The soil physicochemical properties (pH, C/N ratio, soil OM content) did not directly correlate with the soil F/B ratio, but the changes in the C/N ratio along with land-use change were found to explain 16% of the variation in the effect size. Thus, the outcomes of the meta-analysis are consistent with the conclusions of Fierer et al. (2009), suggesting that the soil C/N ratio (or shifts associated with land-use change) predicts the soil F/B ratio most reliably from among the generally measured soil

abiotic parameters. Therefore, it is reasonable to follow the changes in the soil C/N ratio under restorative land use practices as an indicator of the energetic resource shift in microbial communities.

4.5 Economic benefits of ecosystem services on urban areas

The analysis of urban ecosystems was left relatively undermined in the Millenium Ecosystem Assessment (2005) presumably due to small global land coverage of urban areas (there: 2.8 % of land surface area). There are a few papers that include the assessment of monetary value of urban ecosystem services (e.g. McPherson et al., 1999, Nowak et al., 2007, Jim and Chen, 2009). The conducted research has focused mainly on urban forests with estimated value of ecosystem services such as pollutant removal, carbon storage, storm water reduction, recreation and health promoting effects. The monetary value estimated (US$ ha urban forest^{-1} year^{-1}; Elmqvist et al., manuscript) of these ecosystem services range from 10.000 US$ of Modesto forest, CA (McPherson et al., 1999) to over 35.000 US$ value of forest in Guangzhou urban area (Jim and Chen, 2009). The carbon sequestration value of Lahti municipal urban forests (circa 5000 ha) could be approximately 3.26 million EUR for the coming 30-years period (until 2039) in a hypothetical situation with an agreement of principles of international forest carbon sequestration (IFCS) program (Indufor Ltd. and Simosol Ltd., 2011). The annual CO_2 sequestration value would be roughly 22 EUR ha urban forest^{-1} year^{-1} with current management regimes regulated by FSC group certificate (Indufor Ltd. and Simosol Ltd., 2011).

McPherson & Simpson (2002) estimated that the benefit:cost ratios of urban forest in two Californian cities, Modesto and Santa Monica, were 1.85:1 and 1.52:1, respectively. In their analysis the net benefits of urban trees (i.e. energy savings of nearby buildings, reduction of CO_2 emissions, air quality benefits, stormwater reduction, aesthetics) overcame the net costs (i.e. tree planting, pruning, tree removal, sidewalk repair, leaf cleanup) by 35 - 45 % (McPherson & Simpson, 2002). However, the individual evaluations should not be compared directly due to difference in their selection of analysed ecosystem services, and economic assessment methods used.

It is presumable, that because human health effects have often been ignored (Elmqvist et al., manuscript), the current research has substantially underestimated the monetary value of urban ecosystems. This warrants more research on the obvious benefits by the urban green space to recreational and health effects.

5. CONCLUSIONS AND PERSPECTIVES

Urban ecosystems are best described as human-dominated hybrids, unique systems with coupled social and ecological components (Harrison and Burgess, 2003, Alessa and Chapin, 2008, Pickett and Cadenasso, 2009). To maintain the ever-growing human population, there is an increasing demand to restore the functionality and biodiversity of urbanized ecosystems (Pavao-Zuckermann and Byrne, 2009). Furthermore, to generate the most from urban ecological research, the scientific results should be brought into the sociological context.

Urban greening, such as the building of green spaces in the urban environment, has recently been presented as an integrative tool for sustainable city planning by several scientists (Lorenz and Lal, 2009, Bowler et al. 2010, Dvorak and Volder, 2010). The scientific understanding of the multiple ecosystem services provided by these completely

artificial biological systems, such as green roofs and stormwater retention ponds, is still in its infancy (Dvorak and Volder, 2010). In particular, a vast amount of basic and applied ecological ecosystem research is needed to address this knowledge gap. This thesis adds to accumulating evidence of the usefulness of different plant traits in modifying the functionality of ecosystems.

The presumably N conservative plants *H. lanatus*, *C. vulgaris* and *P. abies* created a conservative belowground system, which also effectively diminished the nitrogen leaching losses when grown together with more leaky *L. corniculatus* plants.

Along with the improved biogeochemical management of urban spaces (Lorenz and Lal, 2009), the revegetation and restoration of urban green areas has a multitude of sociological impacts (Nilsson et al. 2007, Peters et al. 2010). The social cohesion of culturally diverse cities and towns may be enhanced by a conscious, yet open design of urban parks with a focus on the democratic facilitation of social interactions (Pickett and Cadenasso 2008, Peters et al. 2010). The adverse effects of urban social polarization may be either diminished or enhanced depending on the practices used in the restoration of urban green spaces (Newman 2008, Dale and Newman 2009). The selection of urban restorative targets that include both social and ecological goals with minimum political pressure should help in establishing a more inclusive approach to revitalization of the urban environment (Newman, 2008). It is necessary to identify the landscapes with convergent social and ecological values, which may be studied, for instance, with spatial cross-correlation using survey data on people's perceptions of the local environment contrasted with key ecosystem parameters, such as NPP (Alessa et al. 2008). The performed meta-analysis (IV) confirmed that soil F/B and C/N ratios are sensitive parameters for restorative land-use changes, highlighting their importance as ecosystem development indicators.

Although the increasing human population density and the spread of urban-type land use is placing enormous pressure on ecosystems, the concentration of human impacts in urban areas may also give new possibilities to restore and preserve the valuable natural areas of rural landscapes with fewer inhabitants. The will to conserve valuable rural landscapes might, however, be paradoxically dependent on the relationship of city dwellers with urban nature (Dunn et al. 2006, Lopez et al. 2007). A reappraisal of urban green spaces as a land use priority is thus important not only for the sake of the multiple ecosystem services produced, but it may be a prerequisite for successful conservation of more remote, valuable habitats.

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